HERMAN de JONG

Institute for Taxonomic Zoology, Amsterdam

THE PHYLOGENY OF THE *NEPHROTOMA FLAVESCENS* SPECIES GROUP (DIPTERA: TIPULIDAE)

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The phylogeny of the currently recognized 22 species and subspecies of the west Palaearctic *Nephrotoma flavescens* species group (Diptera, Tipulidae) is analysed on the basis of 50 morphological characters. The results of the present study are compared with the phylogeny of the *flavescens* group published by Oosterbroek (1980). A synopsis of the distribution of the species and subspecies is given.

H. de Jong, Department of Entomology, Institute for Taxonomic Zoology (Zoological Museum), Plantage Middenlaan 64, 1018 DH Amsterdam, The Netherlands.

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In this paper I will discuss the phylogenetic relationships of the 22 species and subspecies of the *Nephrotoma flavescens* species group sensu Oosterbroek (1980).

The concept of the *flavescens* group adopted here is in accordance with the views of Oosterbroek (1980, 1982). A list of the 22 species and subspecies of the *flavescens* group as recognized in the present paper is given in table 1. A systematic revision of the twenty species and subspecies of the *flavescens* group known at that time was incorporated in Oosterbroek (1978). Subsequently, Oosterbroek (1982) introduced *N. cretensis* and *N. guestfalica hartigiana* as new members of the group. Oosterbroek (1985a) furthermore included the Japanese species *N. subpallida* Alexander in the *flavescens* group. For reasons explained below (section 'Discussion of adopted phylogeny'), I do not accept this combination. An as yet unnamed species, known of female specimens originating from northern Algeria and northern Tunisia, awaits description until the male sex becomes available. It is not included in the phylogenetic analysis of the present paper.

The phylogeny of the *flavescens* group is analysed as part of a research project on the historical biogeography of the western Mediterranean (see De Jong in press). Previously, Oosterbroek (1980) presented a phylogenetic analysis of this species group, but additional information on the distribution of certain characters within *Nephrotoma* prompted a reconsideration of Oosterbroek's conclusions. In the section 'Discussion of adopted phylogeny', I will compare the results of the present study with Oosterbroek's phylogenetic analysis of the *flavescens* group.

The *flavescens* group has an essentially west Palaearctic distribution, with most of its species and subspecies being confined to the Mediterranean sub-

Table 1. The species and subspecies of the *Nephrotoma flavescens* species group as recognized in this paper. + = examined; - = not examined. Females of an as yet undescribed species are known from north Algeria and north Tunisia.

	♂	♀
appendiculata appendiculata Pierre, 1919	+	+
appendiculata pertenua Oosterbroek, 1978	+	+
astigma Pierre, 1925	+	+
beckeri Mannheims, 1951	+	+
cretensis Oosterbroek, 1982	+	+
exastigma Oosterbroek, 1978	+	+
flavescens Linnaeus, 1758	+	+
fontana Oosterbroek, 1978	+	+
guestfalica guestfalica Westhoff, 1879	+	+
guestfalica hartigiana Oosterbroek, 1982	+	+
guestfalica surcoufi Pierre, 1925	+	+
lempkei Oosterbroek, 1978	+	+
minuscula Mannheims, 1951	+	+
nasuta Oosterbroek, 1975	+	+
quadrifaria quadrifaria Meigen, 1804	+	+
quadrifaria farsidica Savchenko, 1957	-	+
saccai Mannheims, 1951	+	+
schaeuffelei Mannheims, 1964	+	+
spatha Oosterbroek, 1975	+	+
submaculosa Edwards, 1928	+	+
sullingtonensis Edwards, 1938	+	+
theowaldi Oosterbroek, 1978	+	+

Fig. 1. Distribution of the *Nephrotoma flavescens* species group.

region (fig. 1). The distribution range of six representatives of the *flavescens* group extends towards northwest Europe. A single male specimen of the species *flavescens* Linnaeus has been reported from western Greenland (cf. Mannheims & Theowald 1971).

Detailed information on the distribution of the species and subspecies of the *flavescens* group can be found in Oosterbroek (1978: distribution maps of the species and subspecies discussed therein) and Oosterbroek (1982, 1985b: additional distributional data). Oosterbroek & Theowald (1992) summarized the ranges of the Palaearctic Tipulidae, including the members of the *flavescens* group. Distribution maps of each of the species and subspecies of the *flavescens* group will be included in a forthcoming paper dealing with the historical biogeography of the western Mediterranean. A synopsis of the distribution of the members of the *flavescens* group is given at the end of the present paper.

A key to the identification of the species and subspecies of the *flavescens* group (as well as all other western Palaearctic members of *Nephrotoma* known at the time) can be found in Oosterbroek (1979c). The more recently described *N. cretensis* and *N. guestfalica hartigiana* will key out under couplet 13 and couplet 3 respectively. Oosterbroek (1982) listed distinguishing characters for both taxa.

Material, methods and terminology

The majority of specimens used for the present study are preserved in the collection of the Department of Entomology of the Institute for Taxonomic Zoology (Zoological Museum), Amsterdam. Additional material was kindly lent by Dr. Eulalia Eiroa (Department of Animal Biology, University of Santiago de Compostela, Spain). Specimens were usually dry pinned, occasionally material was preserved in alcohol.

As most characters used for the phylogenetic analysis pertain to structures of the terminalia of both sexes, preparations of these parts were made. To this end the specimen was relaxed for a few hours in a humifier, after which the (end of the) abdomen was detached. The removed parts were macerated for about three to five minutes in a nearly boiling 10% KOH solution in a bain-marie. The macerated structures were rinsed with water (several times) and 70% alcohol, upon which they were transferred to a watchglass filled with glycerol. Examination of the terminalia was carried out using a Wild stereomicroscope

with a magnification up to 100×. The drawings were made with the aid of a drawing tube on the microscope. For lasting preservation the terminalia were stored in glycerol in a microvial pinned under the pertaining specimen.

The programs HENNIG86, version 1.5 (Farris 1988) and PAUP, version 3.1.1 (Swofford 1993) were used to analyse the phylogeny. For details on the computational methods employed, see the section 'Discussion of adopted phylogeny'.

The terminology used is largely in accordance with McAlpine (1981). I employ some additional terms to denote details of the male and female terminalia. Tangelder (1985) published a review of the morphology of the terminalia of the Tipulidae, and for further details I refer the reader to her paper. The terms used in the present text are explained in figures 3-10, 13, 14, 30 and 50.

BIOLOGY

The species of the *flavescens* group occur in a variety of habitats, ranging from grassland, gardens, scrubs, deciduous as well as coniferous forests to dry sandy places. Adults are usually on the wing in spring and early summer, although *minuscula* Mannheims

(Cyprus and the Levant) flies as early as the middle of January and records of *flavescens* Linnaeus (central and western Europe) are known from as late as September. The species of the *flavescens* group can be found from sea-level up to 2400 m, the highest altitude recorded for *flavescens* in the Alps.

Several authors described immature stages of members of the group, viz. of *appendiculata appendiculata* Pierre, *flavescens*, *guestfalica guestfalica* Westhoff, *quadrifaria quadrifaria* Meigen, and *submaculosa* Edwards (cf. Brindle 1960, Chiswell 1956, Hemmingsen & Jensen 1972, Theowald 1957, 1967). Oosterbroek (1978) presented details on the biology of each of the then recognized members of the *flavescens* group.

SYSTEMATIC POSITION

Mannheims (1951) separated the west Palaearctic species of *Nephrotoma* with acutely pointed cerci in the female from the remaining species of the genus. Savchenko (1973), largely adopting this major division, included most of the species involved in his *cornicina* species group. The *cornicina* group sensu Savchenko contains the species of *Nephrotoma* that in the male carry an extension on the posterior margin

Table 2. Character state matrix of the species and subspecies of the *Nephrotoma flavescens* species group.

| (Sub)species	Character									
	5	10	15	20	25	30	35	40	45	50
appendiculata	00010	11000	11011	00100	01000	11011	10111	00000	00011	00000
a. pertenua	00010	11000	11011	00100	01000	11011	10111	00000	00011	00000
astigma	10010	00010	10111	10100	01110	01111	11000	10000	00011	01000
beckeri	00110	00000	10001	01110	01000	01010	00010	00000	00011	00010
cretensis	00110	00000	10001	01110	01000	01010	00000	00000	00011	00010
exastigma	10010	00000	10000	00100	01000	01111	00000	00000	00011	01000
flavescens	10010	00010	10111	10100	01110	01011	11000	10000	00011	01000
fontana	00010	00010	11011	00100	01100	01011	10000	00000	00011	00000
guestfalica	00011	00000	10001	10101	00001	01111	00000	01010	00011	10000
g. hartigiana	00011	00000	10001	10101	10001	01111	00000	01010	00011	10000
g. surcoufi	00011	00000	10001	10101	10001	01111	00000	01010	00011	10000
lempkei	10010	00011	10111	10100	01110	01111	11000	10000	00011	01100
minuscula	10010	10100	10011	00100	01000	01011	10111	00000	11011	00001
nasuta	00000	00000	10101	00100	01000	01010	00000	00000	00000	00000
quadrifaria	01000	00000	11011	01100	01000	01111	10010	00101	00101	00000
q. farsidica	01000	00000	11011	01100	01000	01111	10010	00101	00101	00000
saccai	00000	00000	1-001	00100	01000	01010	00010	00000	00010	00000
schaeuffelei	00000	00000	10000	00000	01000	00010	00000	00000	00100	00000
spatha	-0010	00000	10001	10000	01000	01011	00000	00000	00100	00000
submaculosa	10010	00011	10111	10100	01110	01011	11000	10000	00011	01100
sullingtonensis	00010	00010	11011	00100	01000	01011	10000	00000	00011	00000
theowaldi	00010	10100	10011	10100	01000	01011	10111	00000	11011	00001
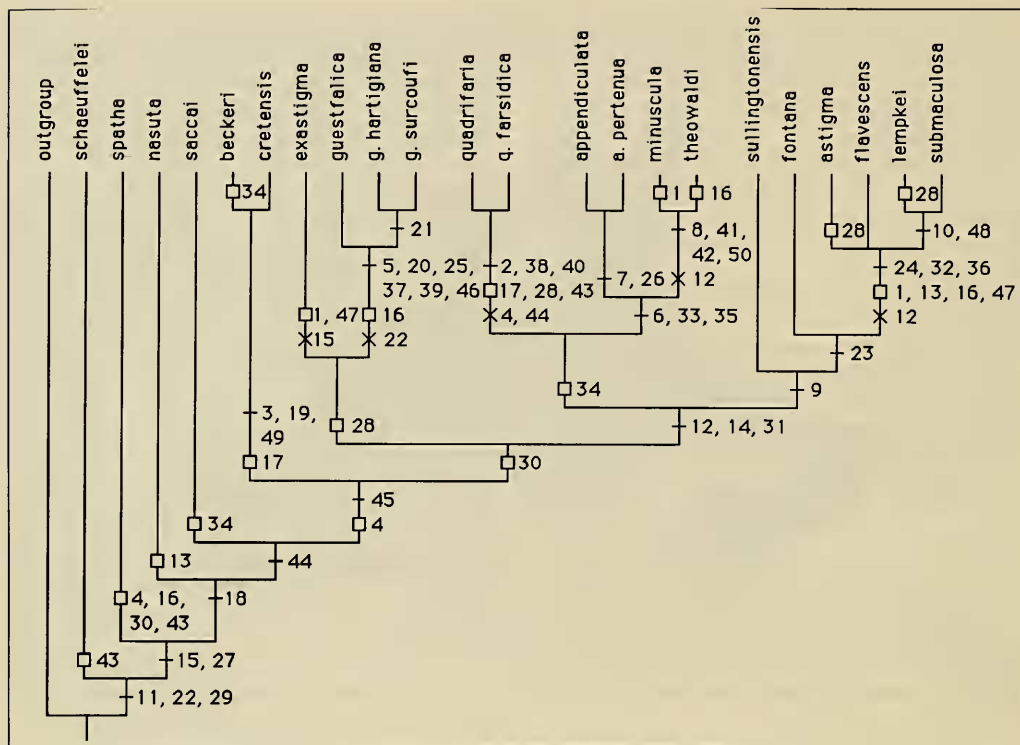
Fig. 2. Consensus tree of two equally parsimonious trees with length 73, consistency index 68 and retention index 84 for the species and subspecies of the *Nephrotoma flavescens* species group. –: synapomorphy; □: homoplasy; ×: reversal.

of sternite eight and that are devoid of bristles on the alar squama. Thus Savchenko excluded the species *guestfalica* Westhoff from his *cornicina* group, meanwhile adding several central and east Palaearctic as well as Oriental species to the group.

Based on three presumed synapomorphies, the *flavescens* species group was first recognized by Oosterbroek (1980) as a subgroup of the *cornicina* group. The monophyly of the *flavescens* group will be further discussed below.

The exact position of the *flavescens* group within the *cornicina* group is not yet established. Oosterbroek (1980) presented a phylogeny of the *cornicina* group, but restricted his analysis to the western Palaearctic species. This approach, for obvious reasons, led to the conclusion that the *flavescens* group is closely related to western Palaearctic species of the *cornicina* group. I have made a preliminary analysis of the phylogeny of the *cornicina* group with the inclusion of some of its east Palaearctic and Oriental members. Results of this investigation show that the *flavescens* group is probably more closely related with east Palaearctic species of the *cornicina* group. An exhaustive analysis of the *cornicina* group, however, was be-

yond the scope of the present paper.

In the phylogenetic analysis of the *flavescens* group I employed the non-*flavescens* group members of the *cornicina* group as the first level outgroup, and the remaining species of *Nephrotoma* as the second level outgroup.

PHYLOGENETIC ANALYSIS

In this section I will discuss the characters used in the phylogenetic analysis of the *flavescens* group. Each character dealt with contains a brief description of its presumed plesiomorphous and apomorphous states, accompanied by their respective codings (0: plesiomorphous, 1: apomorphous). The character state matrix is given in table 2. The resulting cladogram for the *flavescens* group is shown in figure 2 and is discussed in the next section. Autapomorphies of the species and subspecies of the *flavescens* group are given in the appendix to this paper.

Legs
1. – Tarsal claws of male: (0) medial tooth present (fig.

11, arrowed); (1) medial tooth absent (fig. 12) (cf. Oosterbroek 1980: 337, character 24).

The male claws lack the medial tooth in the species *exastigma*, *minuscula* and the members of the clade *astigma* to *submaculosa*. In the species *spatha* the male claws usually bear this tooth, but there are specimens with some or all of the claws toothless. Absence of the medial tooth on the male claw is due to reduction. Females of *Nephrotoma* always have the tarsal claws devoid of teeth.

Species with toothless claws in the male occur frequently in other groups of *Nephrotoma*. According to Oosterbroek (1980: 337) and Tangelder (1985: 160), this character state is usually restricted to smaller monophyletic groups. Referring, among other things, to this character state, Oosterbroek (1980) united the species *exastigma* and *spatha* with the members of the clade *astigma* to *submaculosa*, an interpretation not followed in the present paper.

Wing

2. – Wing-membrane: (0) unmarked; (1) dark crossband running from pterostigma over base of discal cell, crossvein m-cu and apical portion of vein Cu; wing-tip darkened (fig. 13).

The subspecies *quadrifaria quadrifaria* and *quadrifaria farsidica* are distinguished among the members of the *flavescens* group by dark shades below the pterostigma and on the wing-tip. Other species of *Nephrotoma* with similarly marked wings, e.g. *atrostyla* Alexander, *bifusca* Alexander, *gaganboi* Tangelder, and *neopratensis* Alexander, are not closely related with *quadrifaria*.

Male terminalia

3. – Aedeagal guide, apex: (0) gradually tapering towards tip (figs. 5, 14-17, 19-26, 28); (1) with knob-like enlargement at tip (fig. 18).

The species *beckeri* and *cretensis* are sister species that, among other things, are characterized by the shape of the aedeagal guide that terminates in an enlarged tip. Oosterbroek (1982) distinguished this shared derived character state in his discussion on *cretensis* (as 'shape of central part of adminiculum').

4. – Aedeagal guide, gonapophysis: (0) dorsal extension elongate (figs. 14, 16, 17); (1) reduced in length (figs. 5, 15, 18-20, 22-26, 28).

The species *spatha* and the majority of species and subspecies of the clade *beckeri* to *submaculosa* either have a relatively short or completely reduced dorsal extension of the gonapophysis. Contrary to this, both subspecies of *quadrifaria* possess a relatively long dorsal extension (fig. 21). I interpret the character state in *quadrifaria* as a reversal of character state 4(1).

The majority of species of the *cornicina* group have relatively long dorsal extensions of the gonapophyses. Outside the *cornicina* group long dorsal extensions are known in species of the *analis*, *brevipennis*, *dorsalis*, and *pedunculata* species groups of *Nephrotoma* (cf. Oosterbroek 1979b, 1984, 1985a; Tangelder 1983, 1984).

5. – Aedeagal guide, gonapophysis: (0) posterior extension apically rounded (figs. 14-19, 21, 23-26, 28); (1) dorsoventrally flattened and with upcurved acute tip (fig. 20).

The three subspecies of *guestfalica* show the apomorphous state of this character. Within the *flavescens* group, the only other taxa with an acute dorsal tip of the posterior extension of the gonapophysis are both subspecies of *appendiculata* (fig. 22). In the latter two subspecies the posterior extension is mediolaterally flattened (see character 7).

6. – Aedeagal guide, gonapophysis: (0) posterior extension parallel sided or tapering towards tip (figs. 5, 14-17, 19-21, 24-26, 28); (1) spatulate at tip (figs. 22, 23).

The members of the clade *appendiculata* to *theowaldi* have the tip of the posterior extension of the gonapophysis dilated and laterally flattened, the posterior extension thus appearing as a spatulate structure. In both subspecies of *appendiculata* the spatulate part has an acute dorsal tip (fig. 22; see next character), in *minuscula* and *theowaldi* it is rounded off and somewhat downcurved (fig. 23; see character 8).

7. – Aedeagal guide, gonapophysis: (0) tip of posterior extension rounded off when seen in profile (figs. 14-17, 19, 21, 24-26, 28); (1) dorsally with acute tip (fig. 22).
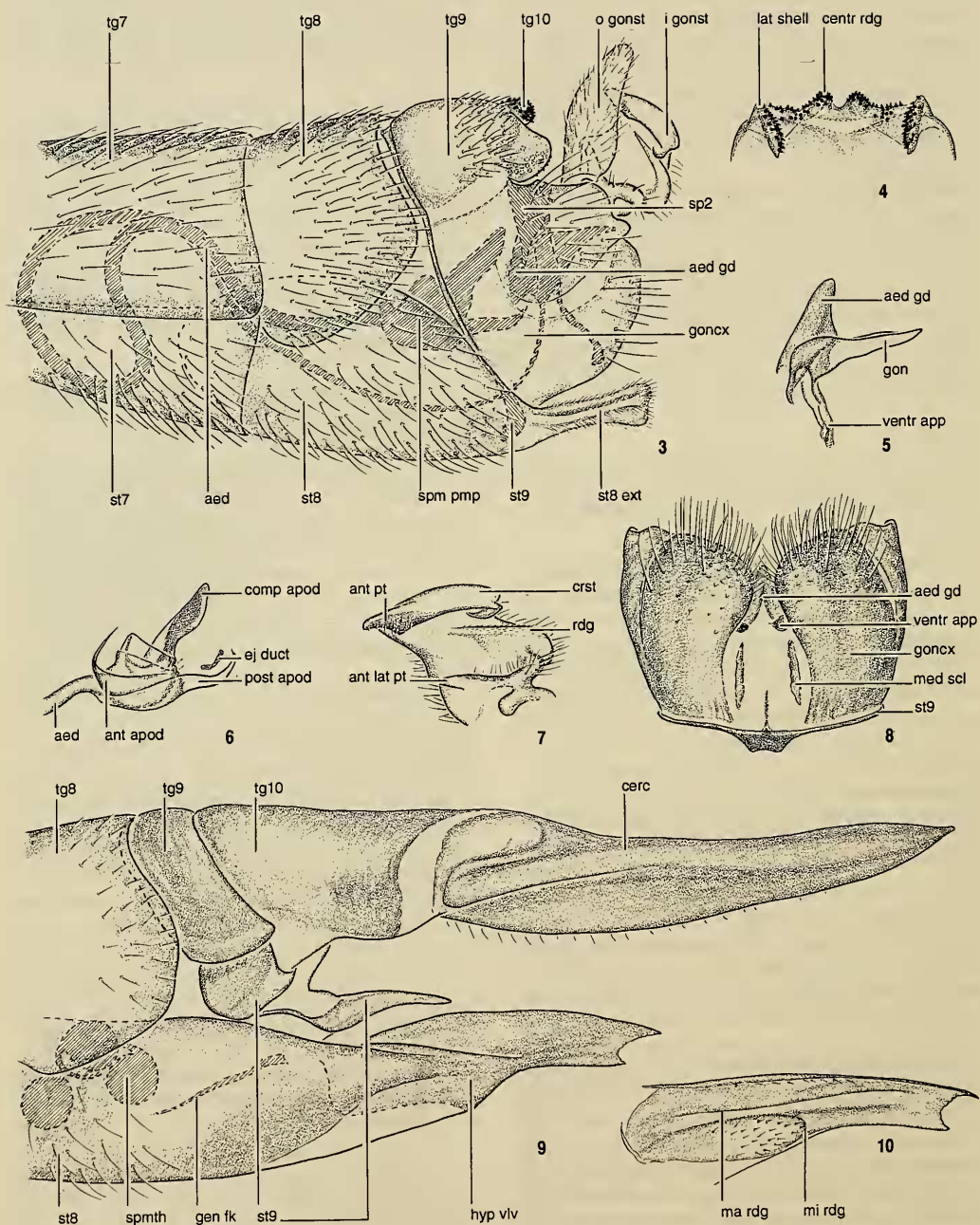
The two subspecies of *appendiculata* show the apomorphous state of this character. The only other members of the *flavescens* group with a dorsally acute posterior extension of the gonapophysis are the three subspecies of *guestfalica* (fig. 20). Here the extension is dorsoventrally flattened and thus of an overall different structure (see character 5).

8. – Aedeagal guide, gonapophysis: (0) ventral margin of posterior extension almost straight when seen in profile (figs. 5, 14-22, 24-26, 28); (1) downcurved at tip (fig. 23) (cf. Oosterbroek 1980: 337, character 25).

The tip of the posterior extension of the gonapophysis is somewhat downcurved in the species *minuscula* and *theowaldi*.

9. – Aedeagal guide, gonapophysis: (0) variously shaped (figs. 14-23); (1) consisting of a mediolaterally flattened and relatively high anterodorsal part and an elongate posterior projection which gradually tapers towards its tip (figs. 5, 24-26, 28).

The species of the clade *sullingtonensis* to *submaculosa* all have a similarly built aedeagal guide plus ap-

pendages, which I interpret as a synapomorphy.

10. – Aedeagal guide, gonapophysis: (0) anterodorsal margin rounded (figs. 26, 27); (1) anterodorsal margin incurved and acutely tipped (fig. 28, 29, arrowed) (cf. Oosterbroek 1980: 337, character 28).

The apomorphous character state separates the species *lempkei* and *submaculosa* from the remainder of the *flavescens* group.

11. – Aedeagal guide, rod: (0) rod present ventral of sperm pump (fig. 30); (1) absent (fig. 31) (cf. Oosterbroek 1980: 332, character 12, as 'adminicular rods').

The species of the *flavescens* group are devoid of rods of the aedeagal guide, although slight vestiges of these structures can be found in individual specimens of the species *beckeri* and *saccai*. Rods of the aedeagal guide are usually present in other species of *Nephrotoma*, including the species of the *cornicina* group outside the *flavescens* group. Reduction of the rods occurs throughout *Nephrotoma* (cf. Oosterbroek 1980: 349, character 5).

12. – Aedeagus: (0) basal, tubular section about 0.50 of total length or longer (figs. 32-35, 37, 39, junction of tubular and branched sections of aedeagus arrowed); (1) basal, tubular section about 0.40 to 0.20 of total length (figs. 36, 38, junction of tubular and branched sections of aedeagus arrowed).

Half of the species and subspecies of the clade *quadrifaria* to *submaculosa* have the branching point of the aedeagus situated before its midlength. Reversal of this state seems to have occurred twice within this clade, once in the ancestor of both *minuscula* and *theowaldi* (cf. fig. 37) and once in the ancestor of the clade *astigma* to *submaculosa* (cf. fig. 39). In the latter clade reversal of character 12(1) coincided with shortening of the aedeagus (see next character).

The presumed plesiomorphous situation of character 12 can be found in non-*flavescens* group members of *Nephrotoma* with a partly tripartite aedeagus, e.g. *alticrista* Alexander, *integra* Alexander, *medioproducta* Alexander, *nigrohalterata* Edwards, and *subpallida* Alexander.

13. – Aedeagus: (0) relatively long and slender (figs. 32, 33, 35-38); (1) short and thick (figs. 34, 39).

The species *nasuta* (fig. 34) and the members of the clade *astigma* to *submaculosa* (cf. fig. 39) have a relatively short aedeagus. Oosterbroek (1980: 336, character 23) also mentioned the species *exastigma* and *spatha* as having a short aedeagus (as 'intromittent organ'). Oosterbroek (1980: 350-351, diagram 1; 391-393, appendix 2B) related the length of the aedeagus with the length of the second abdominal tergite. Contrary to this, the relative proportions of the aedeagus are perhaps better expressed by comparing the length of the aedeagus with its diameter. When the latter procedure is followed and the - arbitrary - limit between relatively long and short is appointed to a quotient of 100 for the total length of the aedeagus and its diameter just after the sperm pump, the aedeagus of both *exastigma* (fig. 35) and *spatha* (fig. 33) turns out to be relatively long (cf. measurements in Oosterbroek 1980, appendix 2A).

In the species of the *cornicina* group outside the *flavescens* group, the aedeagus is a relatively long structure.

14. – Gonocoxite: (0) dorsomedially fused with base of aedeagal guide (fig. 40); (1) separate (fig. 41, gap arrowed).

The species of the clade *quadrifaria* to *submaculosa* show a membranous gap between the base of the aedeagal guide and the adjacent dorsomedial corner of the gonocoxite. In the remaining species of the *flavescens* group both structures are fused, as they are in the other members of the *cornicina* group. Oosterbroek (1980: 337, character 26, as separation of ventral appendages of adminiculum and sternite nine) distinguished the same character state but recognized it in the species of the clade *astigma* to *submaculosa* only. Oosterbroek noted that the gap between both structures can be narrow in other species of *Nephrotoma*. Several species of the *flavescens* group show this latter state, e.g. *fontana*.

15. – Gonocoxite, medisternal sclerotization: (0) fused with ventral appendage of aedeagal guide (fig. 42, connexion arrowed); (1) structures separate from each other (fig. 43, gap arrowed; figs. 8, 47-49).

Figs. 3-10. *Nephrotoma flavescens*, 3-8, male; 9, 10, female. – 3, terminalia, lateral view; 4, tergite 10, ventral view; 5, aedeagal guide, lateral view; 6, sperm pump, lateral view; 7, inner gonostylus, lateral view; 8, sternite 9 and gonocoxites, ventral view; 9, terminalia, lateral view; 10, hypogynial valve, medial view.
Abbreviations: aed: aedeagus; aed gd: aedeagal guide; ant apod: anterior apodeme of sperm pump; ant lat pt: anterolateral part of inner gonostylus; ant pt: anterior part of inner gonostylus; centr rdg: central ridge of tergite 10; cerc: cercus; comp apod: compressor apodeme of sperm pump; crst: crest of inner gonostylus; ej duct: ejaculatory duct; gen fk: genital fork; gon apophysis of aedeagal guide; goncx: gonocoxite; hyp vlv: hypogynial valve; i gonst: inner gonostylus; lat shell: lateral shell of tergite 10; ma rdg: major ridge of hypogynial valve; med scl: medisternal sclerotization; mi rdg: minor ridge of hypogynial valve; o gonst: outer gonostylus; post apod: posterior apodeme of sperm pump; rdg: ridge of inner gonostylus; sp2: lateral remnant of genital bridge; spmth: spermatheca; st7 etc.: sternite 7 etc.; st8 ext: extension of sternite 8; tg7 etc.: tergite 7 etc.; ventr app: ventral appendage of aedeagal guide.

Within the *flavescens* group, *schaeuffelei* and *exastigma* are the only species which have the ventral appendages of the aedeagal guide fused with the medisternal sclerotizations. In all other members of the group these structures are separated by a membranous gap. When the medisternal sclerotizations are well developed, they are united with the appendages of the aedeagal guide in the non-*flavescens* group members of the *cornicina* group.

16. – Gonocoxite, medisternal sclerotization: (0) well developed, large (fig. 42, 44, 46-48); (1) reduced in size, small or absent (figs. 8, 43, 45, 49).

It is assumed that the presence of medisternal sclerotizations is a plesiomorphy within the genus *Nephrotoma* (Oosterbroek 1980: 321; Tangelder 1985: 144). Reduced medisternal sclerotizations occur within the *flavescens* group in the species *spatha* (fig. 43), the three subspecies of *guestfalica* (cf. fig. 45), the species *theowaldi*, and the members of the clade *astigma* to *submaculosa* (figs. 8, 49). The shape of the reduced medisternal sclerotizations varies among these taxa.

17. – Gonocoxite, medisternal sclerotization: (0) not in contact with ventromedial margin of gonocoxite or only so along a relatively short zone (figs. 8, 42, 43, 45, 47-49); (1) fused for more than half its length with gonocoxite (figs. 44, 46).

When in contact with the gonocoxites, the medisternal sclerotizations are usually only fused with these structures near their anterior margins (cf. fig. 47). The sister species *beckeri* (fig. 44) and *cretensis*, and both subspecies of *quadrifaria* (cf. fig. 46) are characterized by a more complete fusion of both structures. I assume that fusion evolved independently in both pairs of taxa.

18. – Inner gonostylus: (0) a projecting posterolateral part present (figs. 50-52, structure arrowed in figs. 51 and 52); (1) posterolateral part reduced (figs. 7, 53-66).

Within the *flavescens* group, the species *schaeuffelei* and *spatha* have a projecting structure placed posterolaterally on the inner gonostylus. I interpret this structure as the homologue of the posterolateral part of the inner gonostylus of other genera and subgenera of Tipulidae. As such it is a plesiomorphy in *Nephrotoma*. In several species of the *flavescens* group its remnant is readily identifiable in the low protuberance covered with long hairs on the posterolateral margin of the inner gonostylus (e.g. *nasuta*, fig. 53; *exastigma*, fig. 57; *appendiculata*, fig. 62; *minuscula*, fig. 63; *sullingtonensis*, fig. 64).

Several members of the *cornicina* group outside the *flavescens* group have a distinct projecting posterolateral extension on the inner gonostylus (fig. 50; cf. Oosterbroek 1980: 330, character 5). Oosterbroek interpreted this character state as an apomorphy of

his *cornicina* subgroup, but considering its occurrence outside and within *Nephrotoma*, it is probably better regarded as a plesiomorphy on this level of analysis.

19. – Inner gonostylus: (0) general shape various, seen in lateral view with relatively short and high anterior part (figs. 7, 50-53, 57-66); (1) general shape similar, in lateral view anterior part and crest appearing in line, elongate and slender (fig. 54).

The inner gonostyli of the species *beckeri* and *cretensis* show a number of features that can be interpreted as apomorphies: the anterior part is acutely bent over laterally (fig. 55; less so in the other members of the *flavescens* group), the anterolateral part is smoothly curved when seen in dorsal aspect (fig. 56; acute in the other species of the *flavescens* group) and the crest is posteriorly produced into an acute tip (fig. 54; the only other representative of the *flavescens* group with an acute crest is the subspecies *guestfalica guestfalica*, fig. 58). Oosterbroek (1982) mentioned the synapomorphous resemblance of the shape of the inner gonostyli of *beckeri* and *cretensis* in his discussion on the latter species.

20. – Inner gonostylus: (0) general shape various, lateral edge toothless (figs. 7, 50-57, 61-66); (1) general shape similar, laterally with edge toothed (figs. 58-60).

The three subspecies of *guestfalica* share some apomorphous peculiarities in the structure of the inner gonostylus: the anterior part is large and produced, while the lateral margin is present as a rim carrying blackish sclerotized points. The inner gonostyli of the subspecies differ in degree of reduction of the dorsal crest (see next character).

21. – Inner gonostylus: (0) crest on anterior part well developed, posteriorly extending (fig. 58); (1) crest reduced in length (figs. 59, 60).

Oosterbroek (1980: 326, character 12) considered a posteriorly produced crest a synapomorphy of the species of the *cornicina* group. A posteriorly produced crest can therefore be interpreted as a plesiomorphy within the *flavescens* group. Reduction of the posterior extension of the crest is found in the subspecies *guestfalica hartigiana* and *guestfalica surcoufi*. In *guestfalica hartigiana* the crest is shortened (fig. 59), in *guestfalica surcoufi* it is completely absent (fig. 60).

The members of the clade *fontana* to *submaculosa* also show reduction of the posterior extension of the crest. Reduction in this clade resulted in a distinct situation and is treated under character 23.

22. – Inner gonostylus: (0) without ridge (fig. 50); (1) with ridge on its lateral side (figs. 7, 51-57, 61-66) (cf. Oosterbroek 1980: 332, character 11).

All members of the *flavescens* group, with the ex-
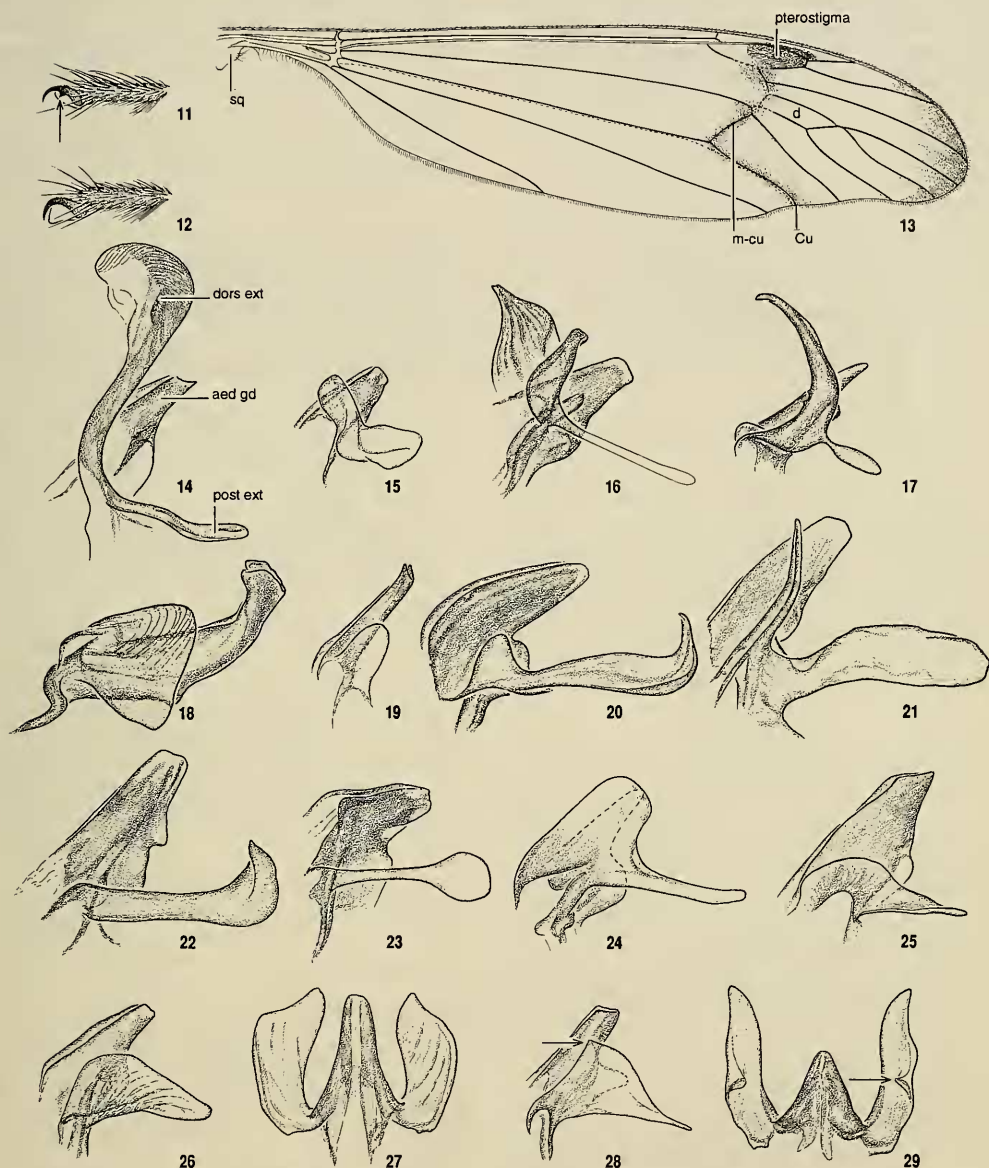
Figs. 11-29. – 11, 12, *Nephrotoma spatha,* male last tarsal segment; 13, *N. quadrifaria,* wing; 14, *N. schaeuffelei,* aedeagal guide and gonapophysis, lateral view; 15, *N. spatha,* idem; 16, *N. nasuta,* idem; 17, *N. saccai,* idem; 18, *N. beckeri,* idem; 19, *N. exastigma,* idem; 20, *N. guestfalica guestfalica,* idem; 21, *N. quadrifaria quadrifaria,* idem; 22, *N. appendiculata appendiculata,* idem; 23, *N. minuscula,* idem; 24, *N. sullingtonensis,* idem; 25, *N. fontana,* idem; 26, 27, *N. astigma,* 26, idem; 27, aedeagal guide and gonapophysis, dorsal view; 28, 29, *N. lempkei,* 28, aedeagal guide and gonapophysis, lateral view; 29, aedeagal guide and gonapophysis, dorsal view.

Abbreviations: aed gd: aedeagal guide; Cu: cubital vein; d: discal cell; dors ext: dorsal extension of gonapophysis; m-cu: medio-cubital crossvein; post ext: posterior extension of gonapophysis; sq: squama.

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ception of the three subspecies of *guestfalica*, are characterized by the presence of a ridge on the posterior part of the inner gonostylus. (Contrary to Oosterbroek's assertion, *nasuta* does have a ridge underneath the crest; cf. fig. 53, arrowed).

Most other species of the *cornicina* group, and all other *Nephrotoma* examined, lack this feature. The only representatives of the *cornicina* group with a ridge-like structure are *cornicina cornicina* Linnaeus, *cornicina sardiniensis* Oosterbroek, and *moravica*
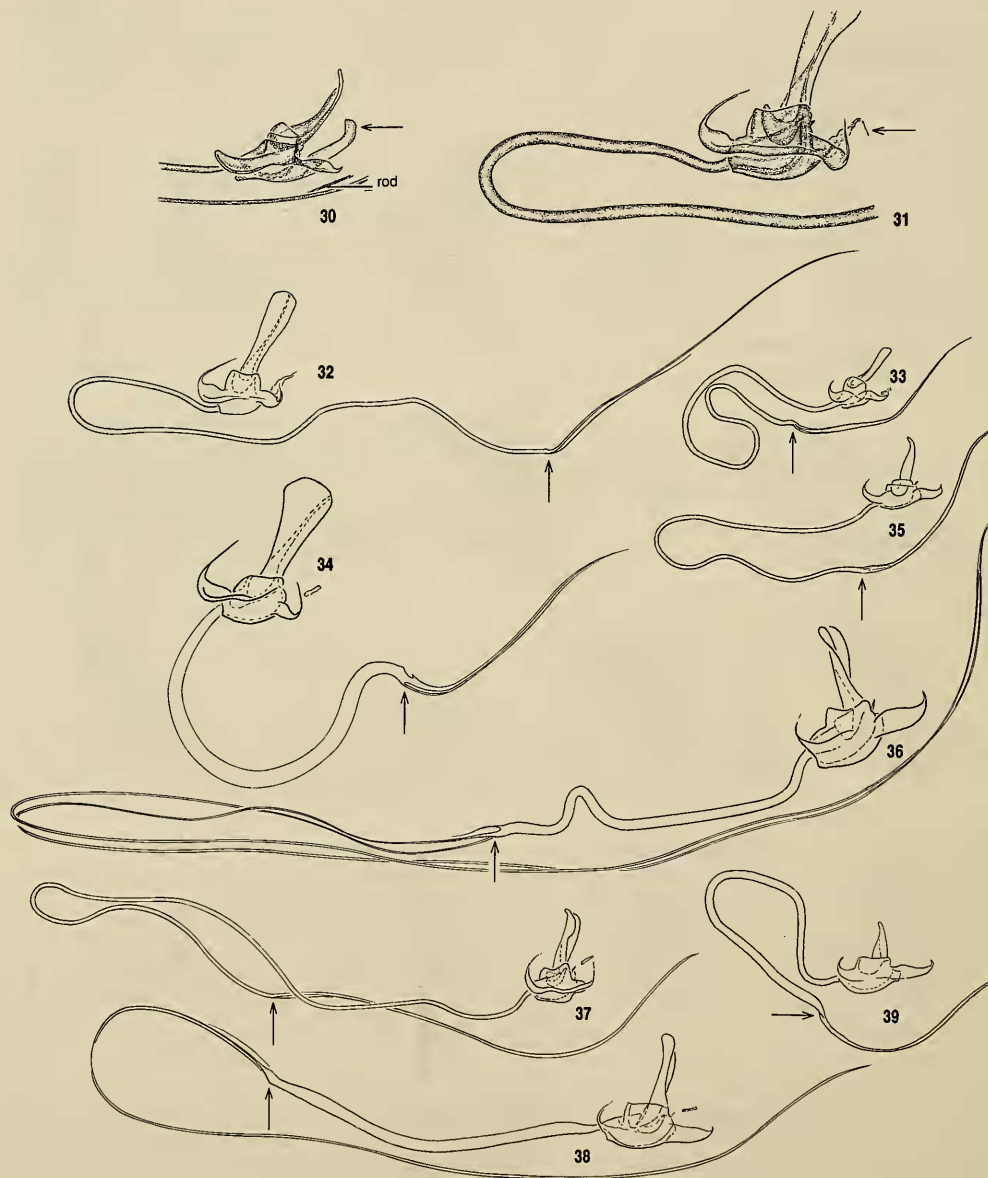
Figs. 30-39. – 30, *Nephrotoma ligulata,* sperm pump and part of aedeagus, lateral view; 31, 32, *N. schaeuffelei,* 31, idem; 32, sperm pump and aedeagus, lateral view; 33, *N. spatha,* idem; 34, *N. nasuta,* idem; 35, *N. exastigma,* idem; 36, *N. quadrifaria quadrifaria,* idem; 37, *N. minuscula,* idem; 38, *N. fontana,* idem; 39, *N. astigma,* idem.
Abbreviation: rod: rod of aedeagal guide.

Martinovský. These three taxa together form a monophyletic group within the *cornicina* group (cf. Oosterbroek 1980). Here the ridge-like structure probably evolved independently of that of the *flavescens* group.

23. – Inner gonostylus: (0) crest on anterior part well developed, posteriorly extending (figs. 52-58, 61-64); (1) crest reduced in length, posteriorly laterally downcurved (figs. 7, 65, 66).

In the clade *fontana* to *submaculosa*, the apomorphous state of this character can be found. Oosterbroek (1980: 337, character 27) recognized this apomorphy for the species of the clade *astigma* to *submaculosa*. I claim that it also applies to the species *fontana* (fig. 65).

24. – Inner gonostylus: (0) ridge without pubescence (figs. 51-57, 61-65); (1) ridge covered with dense pubescence (fig. 7, 66) (cf. Oosterbroek 1980: 332, character 11X).

The species of the clade *astigma* to *submaculosa* are distinguished from the remainder of species and subspecies of the *flavescens* group, by the presence of pubescence on the ridge of the inner gonostylus.

25. – Outer gonostylus: (0) at base with anteromedially directed extension (figs. 67, 69); (1) with elongate ventrolateral extension (fig. 68).

The outer gonostylus of the majority of species of *Nephrotoma* is provided with a more or less well developed anteromedially directed extension at its base. In the three subspecies of *guestfalica* the outer gonostylus basally bears a long ventrolaterally directed extension.

26. – Outer gonostylus: (0) elongate, without strikingly long hairs (figs. 67, 68); (1) broad, long haired along posterior margin, with longest hairs about as long as width of outer gonostylus (fig. 69).

The outer gonostylus of the majority of species of *Nephrotoma* is a rather slender structure when seen in lateral view, covered with moderately long hairs. In the two subspecies of *appendiculata*, the outer gonostylus is relatively broad and bears long hairs along its posterior margin.

27. – Sperm pump: (0) sclerotized part of ejaculatory duct attached to sperm pump (figs. 30, 31, 70, ejaculatory duct arrowed); (1) membranous gap between sperm pump and sclerotized part of ejaculatory duct (figs. 6, 71-73, 75) (cf. Oosterbroek 1980: 332, character 14).

In the *flavescens* group the sclerotized part of the ejaculatory duct is attached to the sperm pump in the species *schaeuffelei* only (figs. 31, 70). In the other species and subspecies of the group there either is a membranous gap between the body of the sperm

pump and the sclerotized part of the ejaculatory duct or the ejaculatory duct is not sclerotized at all (see next character). The gap between the sperm pump and the sclerotized part of the duct is narrow in the species *beckeri* (fig. 73), in the other relevant species and subspecies of the *flavescens* group it is wider (figs. 6, 71, 72, 75).

Oosterbroek (1980: 326, character 11) recognized the presence of a midposterior appendage to the sperm pump (as 'aedeagus') as a synapomorphy for the *cornicina* group. I interpret the midposterior appendage as a sclerotization of the wall of the ejaculatory duct (seminal duct of Byers 1961). The species of the *cornicina* group outside the *flavescens* group have this sclerotized structure well developed, being attached to the sperm pump (fig. 30).

28. – Sperm pump: (0) vestige of sclerotized portion of ejaculatory duct present (figs. 6, 71-73, 75); (1) absent (fig. 74).

As mentioned under the preceding character, some members of the *flavescens* group do not show a trace of sclerotization of the ejaculatory duct. The species and subspecies involved are *exastigma* (fig. 74), the subspecies of *guestfalica* and *quadrifaria*, and *astigma* and *lempkei*. It seems that reduction of the sclerotization of the ejaculatory duct evolved along several lineages and to various degrees within the *flavescens* group.

29. – Sperm pump, anterior apodemes: (0) without long membranous extensions at tip (fig. 30); (1) with long membranous extensions at tip (fig. 6, 31, 71).

All members of the *flavescens* group are characterized by the possession of long translucent extensions at the tips of the anterior apodemes of the sperm pump. I did not find such extensions in species of *Nephrotoma* outside the *flavescens* group.

30. – Sperm pump, anterior apodeme: (0) broad, bulging in dorsal view (figs. 70, 73); (1) reduced to narrow strip (figs. 72, 74, 75).

The anterior apodemes of the sperm pump are usually well developed in *Nephrotoma*. Within the *flavescens* group, reduced anterior apodemes are present in the species *spatha* (fig. 72) and the members of the clade *exastigma* to *submaculosa* (figs. 74, 75).

Oosterbroek (1980: 333, character 15) also recognized a reduction of the anterior apodemes (as 'lateral appendages of the aedeagus') as an apomorphy in the *flavescens* group. The largest anterior apodemes in the *flavescens* group are found in the species *nasuta* and *saccai*. Oosterbroek distinguished a monophyletic group composed of the remainder of species and subspecies of the *flavescens* group on account of this feature. As relatively large anterior apodemes are also
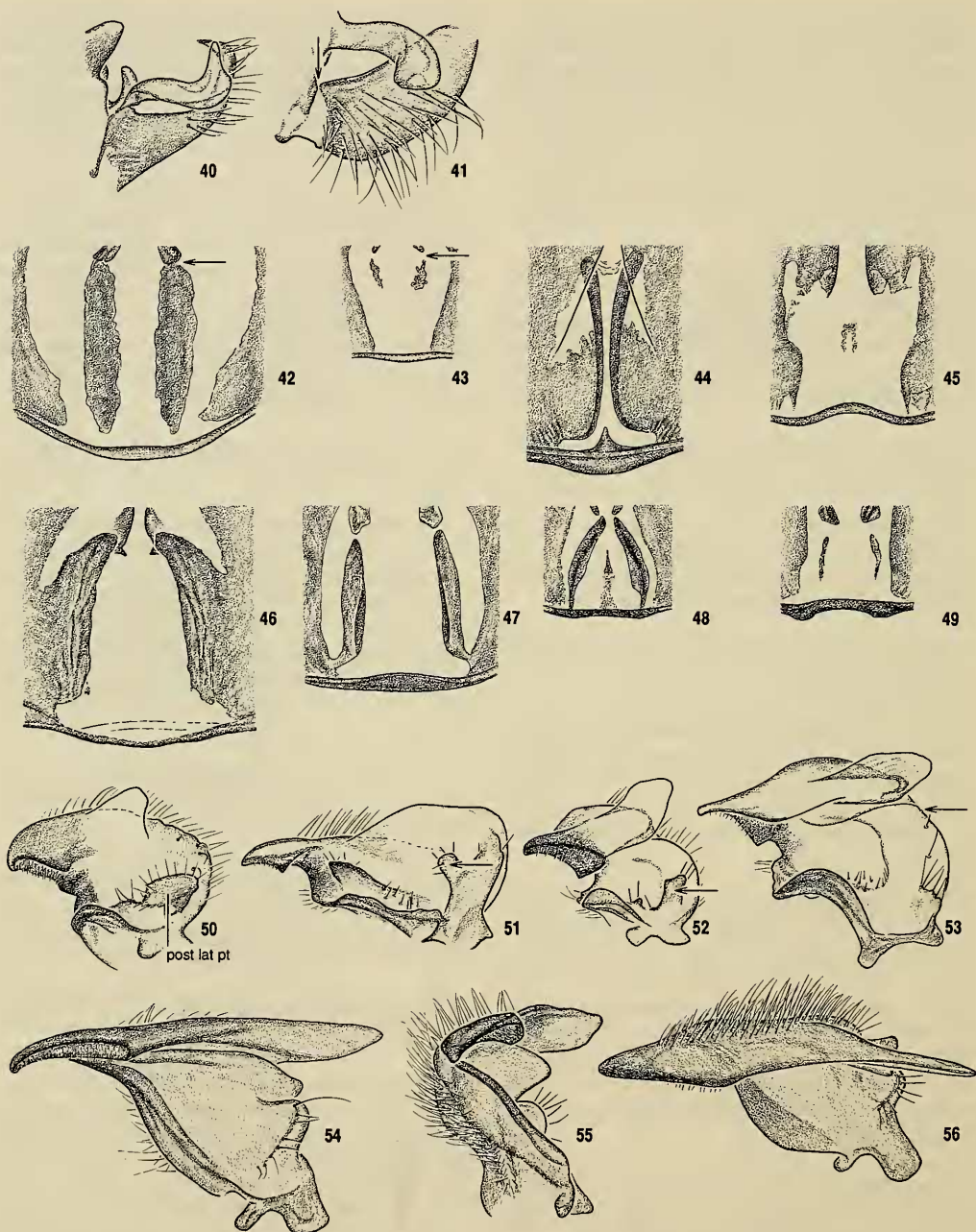
Figs. 40-56. – 40, *Nephrotoma guestfalica guestfalica*, base of aedeagal guide in part plus right gonocoxite, posterolateral view; 41, *N. quadrifaria quadrifaria*, idem; 42, *N. schaeuffelei*, male sternite 9, gonocoxites and medisternal sclerotizations, ventral view; 43, *N. spatha*, idem; 44, *N. beckeri*, idem; 45, *N. guestfalica guestfalica*, idem; 46, *N. quadrifaria quadrifaria*, idem; 47, *N. appendiculata appendiculata*, idem; 48, *N. minuscula*, idem; 49, *N. astigma*, idem; 50, *N. ligulata*, inner gonostylus, lateral view; 51, *N. schaeuffelei*, idem; 52, *N. spatha*, idem; 53, *N. nasuta*, idem; 54-56, *N. beckeri*, inner gonostylus, 54, lateral view; 55, anterior view; 56, dorsal view.
Abbreviation: post lat pt: posterolateral part of inner gonostylus.

present in *schaeuffelei, beckeri,* and *cretensis,* I do not adopt this interpretation.

31. – Sperm pump, compressor apodeme: (0) deeply incised (fig. 76); (1) almost entire, dorsal margin either slightly concave or entirely convex (fig. 77).

Within the *flavescens* group, the species and subspecies of the clade *quadrifaria* to *submaculosa* have a compressor apodeme which consists of an undivided structure.

32. – Sperm pump, compressor apodeme: (0) entire, with midposterior keel; (1) without midposterior keel.

The more basal species and subspecies of the clade *quadrifaria* to *submaculosa* have the compressor apodeme provided with a well developed midposterior keel. The keel is completely reduced in the species of the clade *astigma* to *submaculosa.*

33. – Sperm pump, posterior apodeme: (0) yellowish coloured, elongate (figs. 6, 30, 31, 70-72, 74); (1) dark coloured and short (fig. 75).

Dark sclerotized, short posterior apodemes occur in the species of the clade *appendiculata* to *theowaldi* of the *flavescens* group. The remainder of species of the group have the posterior apodemes less heavily sclerotized.

In the clade *appendiculata* to *theowaldi* sclerotization of the posterior apodemes coincides with reduction of these structures. Oosterbroek (1980: 336, character 22) recognized short posterior apodemes (as 'posterior appendages of the aedeagus') as an apomorphy of the clade *appendiculata* to *theowaldi.* However, reduced posterior apodemes are also known in the species *nasuta* and *beckeri* (fig. 73). The apodemes in the two latter species are not blackish sclerotized.

34. – Sp2: (0) haired (figs. 78, 83, arrowed); (1) bare (figs. 79-82).

As in the majority of other species of the *cornicina* group, most members of the *flavescens* group have the posteromedial margin of sp2 near midlength provided with a concentration of hairs. Within the *flavescens* group, these hairs are absent in the species *saccai* (fig. 79), *beckeri* (fig. 80) and in the clade *quadrifaria* to *theowaldi* (cf. figs. 81, 82).

35. – Sp2: (0) variously shaped (figs. 78-81, 83); (1) similar (fig. 82).

The species of the clade *appendiculata* to *theowaldi* possess a similarly built sp2. The bare structure has the dorsal part well developed and anteriorly protruding, while the ventral part is present as a straight ventromedially directed appendix.

36. – Sp2: (0) variously shaped (figs. 78-82); (1) similar (fig. 83).

In the clade *astigma* to *submaculosa* the sp2 structure has a small and protruding dorsal part, while it is slightly produced posteriorly near midlength at the point of insertion of the hairs. The ventral part is straight and gradually tapers towards its tip.

37. – Sternite 8: (0) with posterior extension (figs. 3, 84, 86); (1) without (fig. 85).

The only members of the *flavescens* group without an extension on the posterior margin of sternite 8 are the three subspecies of *guestfalica.* All other species of the *cornicina* group have a well-developed posterior extension of sternite 8.

38. – Sternite 8: (0) posterior extension dorsoventrally compressed (fig. 84); (1) laterally compressed (fig. 86).

The extension of sternite 8 is short and laterally compressed in both subspecies of *quadrifaria.* The majority of species of the *cornicina* group have the extension either dorsoventrally flattened or rounded in cross-section. Only *cornicina cornicina, cornicina sardiniensis* and *moravica* have the extreme apex of the extension laterally compressed. However, in these taxa the posterior extension of sternite 8 is dorsoventrally flattened at its base and elongate.

39. – Tergite 10: (0) variously shaped (figs. 3, 4, 89-94); (1) consisting of two cup-shaped structures provided with black spines along their anteromedial and posterior margins, each carrying an acute lateral extension (figs. 87, 88).

The three subspecies of *guestfalica* are characterized by their uniquely shaped tergite 10. Oosterbroek (1980: 336, character 17P) considered *guestfalica* and *quadrifaria* sister taxa, a relationship presumed, among other things, to be supported by similarities in the structure of tergite 10 (as 'extension of tergite 9'). In my opinion the shape of tergite 10 in *quadrifaria* (figs. 89, 90) has no apomorphy in common with that of *guestfalica* (figs. 87, 88).

40. – Tergite 10: (0) variously shaped, with relatively narrow medial incision, caudally directed (figs. 3, 4, 87, 88, 91-94); (1) posteriorly widely emarginate, caudodorsally directed (figs. 89, 90).

The two subspecies of *quadrifaria* are characterized by their peculiarly shaped tergite 10.

41. – Tergite 10: (0) central ridges posteriorly not or only slightly produced (fig. 91); (1) central ridges posteriorly produced (fig. 93) (cf. Oosterbroek 1980: 336, character 17S; tergite 10 as 'extension of tergite 9').

The central part of tergite 10 protrudes only moderately in most species of the *flavescens* group. Only

minuscula and *theowaldi* show a posterior elongation of this part of tergite 10.

42. – Tergite 10: (0) lateral shells rounded along ventral margin when seen in lateral view (fig. 92); (1) ventral margin truncate (fig. 94).

The species *minuscula* and *theowaldi* are the only members of the *flavescens* group which have the ventral margin of the lateral shells of tergite 10 straight. In the other members of the group, as well as in most other species of *Nephrotoma*, this margin is rounded.

Female terminalia
43. – Cercus: (0) long, well-developed, gradually tapering towards tip (fig. 99); (1) reduced in length, tip rounded off (figs. 95, 97, 106).

Within the *flavescens* group a shortened, blunt-tipped cercus is known in the species *schaeuffelei* (fig. 95), *spatha* (fig. 97), and the two subspecies of *quadrifaria* (fig. 106). Besides being reduced in length, the cercus of both subspecies of *quadrifaria* is also reduced in height. In the remainder of species and subspecies of the *flavescens* group the cercus is long and either gradually tapers towards the tip (fig. 99), or is produced into a nipple-like extension (see next character).

Oosterbroek (1980: 326, character 14 and page 328, character 1) listed the presence of pointed cerci in the female as one of the synapomorphies of the *cornicina* group. The cerci in this group are also more robust than is usual in *Nephrotoma* (cf. Savchenko 1973: 35, 119). The plesiomorphous form of the cercus in the *cornicina* group can be found in supposedly basal species like *forcipata* Pierre and *ligulata* Alexander. Here the well-developed cercus gradually tapers towards its tip. In the *flavescens* group a similarly shaped cercus is found in the species *nasuta* (fig. 99) and in the as yet undescribed species from Algeria and Tunisia. The cercus of *nasuta* and the north-west African species probably represents the plesiomorphous form in the *flavescens* group.

44. – Cercus: (0) gradually tapering towards tip (fig. 99); (1) tip produced into a nipple-like extension (figs. 9, 101).

With the exception of both subspecies of *quadrifaria*, the species and subspecies of the clade *saccai* to *submaculosa* are characterized by the possession of a nipple-like projection of the tip of the cerci. (The nipple-like projection is frequently worn off in older specimens).

As stated under the preceding character, the plesiomorphous condition of the female cercus in the *flavescens* group is probably represented by a moderately pointed structure as found in *nasuta* (fig. 99).

45. – Hypogynial valve: (0) tip entire, with ventral mar-

gin evenly convex (figs. 96, 98, 100, 102); (1) tip irregular, appearing to be broken off (figs. 9, 10, 103-105, 108-110) (cf. Oosterbroek 1980: 333, character 16).

The species of the clade *beckeri* to *submaculosa* show the apomorphous condition of this character. Within the *cornicina* group a similar situation is known in the non-*flavescens* group species *saghaliensis* Alexander, where it apparently evolved independently (cf. fig. 6 of Oosterbroek 1985a. Fig. 13 of Oosterbroek 1985a, depicts a damaged specimen of *esakii* Alexander in which the tip of the hypogynial valve is actually broken off; in intact specimens of this species the hypogynial valve terminates in an acute tip).

The basal species of the *flavescens* group, as well as the other members of the *cornicina* group, have slender, reduced hypogynial valves of which the ventral margin of the tip is entire (cf. figs. 96, 98, 100, 102).

46. – Hypogynial valve: (0) dorsal margin continuous (figs. 9, 10, 96, 98, 100, 102-104, 107-110); (1) dorsal margin with posteriorly directed point at about two-thirds of its length (fig. 105).

The three subspecies of *guestfalica* are, among other things, characterized by their apomorphously shaped hypogynial valves.

47. – Hypogynial valve: (0) major and minor ridges basally in contact with each other (figs. 102, 103, 108); (1) separate (figs. 10, 109, 110).

In the Tipulidae there are usually two ridges on the medial side of the hypogynial valve, a major (dorsal) and a minor (ventral) one (cf. fig. 10). As this situation is found also in the majority of species of *Nephrotoma*, I agree with Oosterbroek (1980: 326), who interpreted the presence of two ridges as a plesiomorphy for the genus. Tangelder (1985: 151), however, considered the same character state an apomorphy within *Nephrotoma*.

When present, both ridges are usually separate, like they are in the species *schaeuffelei* of the *flavescens* group (fig. 96). A partly or entirely reduced minor ridge is frequently found in the *flavescens* group, e.g. in *schaeuffelei* (fig. 96), *spatha* (fig. 98), *nasuta* (fig. 100) and the subspecies of *guestfalica* (fig. 105). In other species of the group the minor ridge is well developed and both major and minor ridges are fused at their base, e.g. in *saccai* (fig. 102), *beckeri* (fig. 103), *cretensis*, the subspecies of *appendiculata* and in *fontana* (fig. 108).

In the sistergroup of *fontana*, viz. the clade *astigma* to *submaculosa*, both ridges are separate. Judged by the situation in the nearest outgroups of this clade, this trait can be interpreted as an apomorphy (cf. figs. 109, 110). The species *exastigma* (fig. 104) also has the ridges separate, probably as the result of a secon-
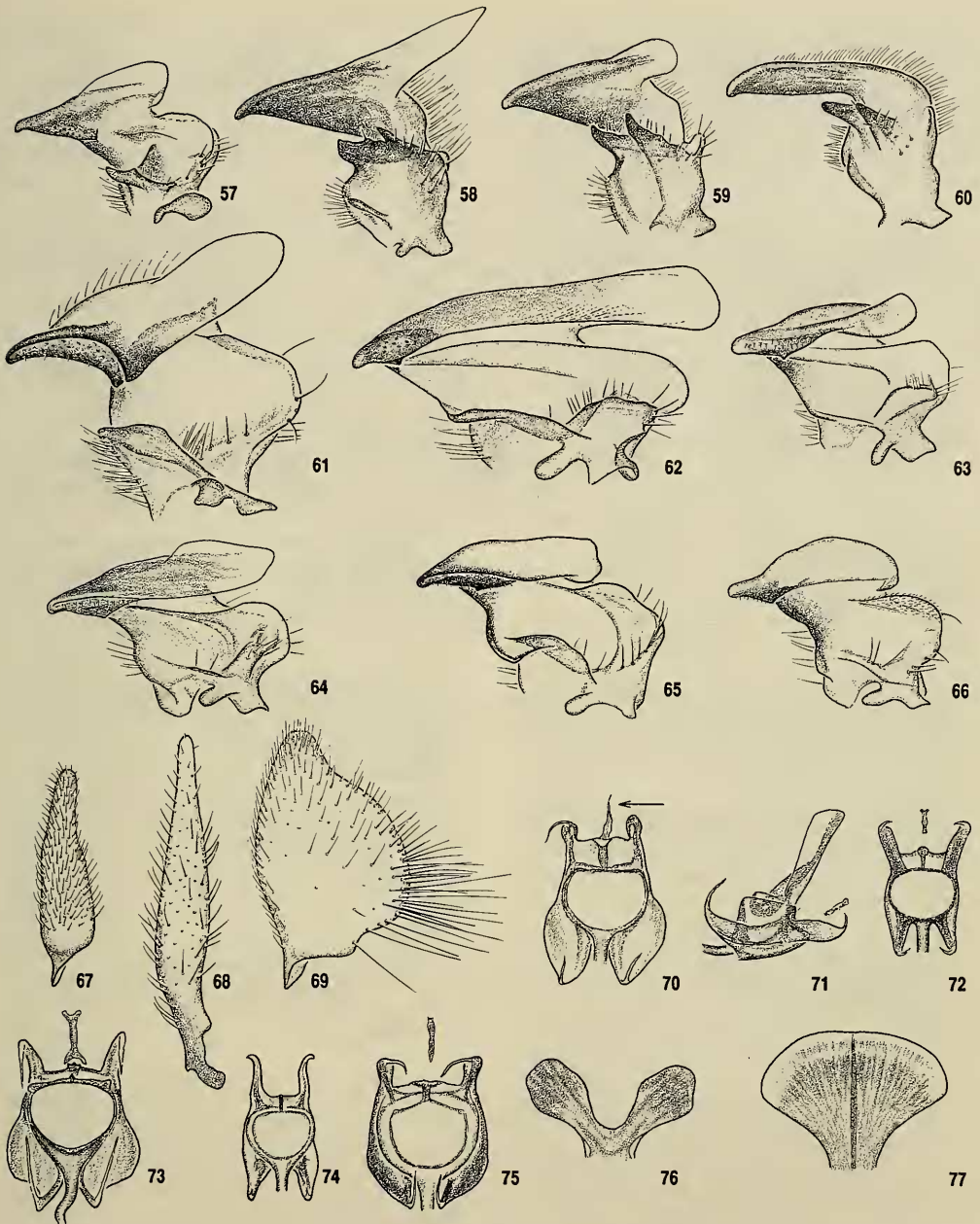
Figs. 57-77. – 57, *Nephrotoma exastigma,* inner gonostylus, lateral view; 58, *N. guestfalica guestfalica,* idem; 59, *N. guestfalica hartigiana,* idem; 60, *N. guestfalica surcoufi,* idem; 61, *N. quadrifaria quadrifaria,* idem; 62, *N. appendiculata appendiculata,* idem; 63, *N. minuscula,* idem; 64, *N. sullingtonensis,* idem; 65, *N. fontana,* idem; 66, *N. astigma,* idem; 67, *N. exastigma,* outer gonostylus, lateral view; 68, *N. guestfalica guestfalica,* idem; 69, *N. appendiculata appendiculata,* idem; 70, *N. schaeuffelei,* sperm pump, dorsal view, compressor apodeme omitted; 71, 72, *N. spatha,* 71, sperm pump, lateral view; 72, sperm pump, dorsal view, compressor apodeme omitted; 73, *N. beckeri,* idem; 74, *N. exastigma,* idem; 75, *N. appendiculata appendiculata,* idem; 76, *N. guestfalica guestfalica,* compressor apodeme, anterior view; 77, *N. quadrifaria quadrifaria,* idem.
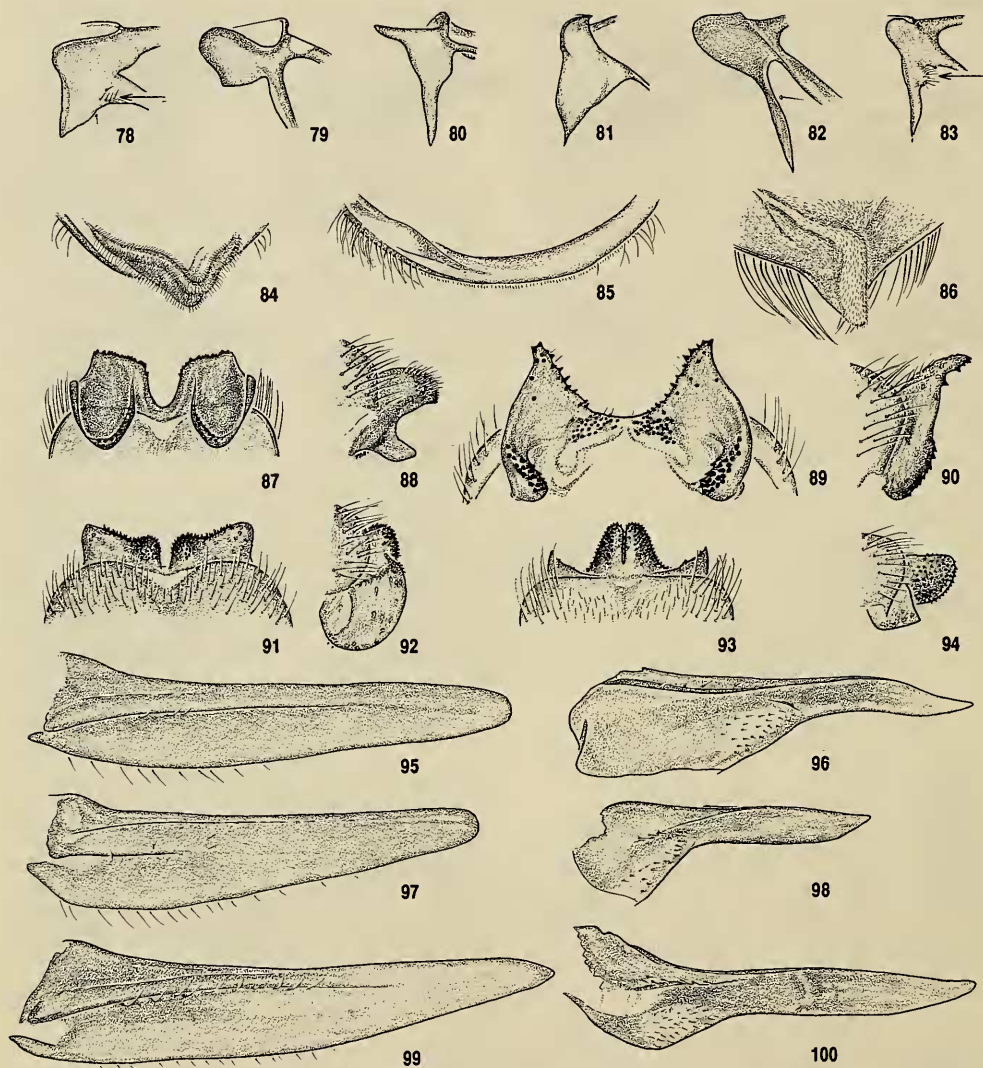
Figs. 78-100. – 78, *Nephrotoma nasuta,* sp2, medial view; 79, *N. saccai,* idem; 80, *N. beckeri,* idem; 81, *N. quadrifaria quadrifaria,* idem; 82, *N. appendiculata appendiculata,* idem; 83, *N. astigma,* idem; 84, *N. exastigma,* posterior margin of male sternite 8, posterolateral view; 85, *N. guestfalica guestfalica,* idem; 86, *N. quadrifaria quadrifaria,* idem; 87, 88, *N. guestfalica guestfalica.* 87, male tergite 10, ventral view; 88, male tergite 10, lateral view; 89, 90, *N. quadrifaria quadrifaria,* 89, male tergite 10, ventral view; 90, male tergite 10, lateral view; 91, 92, *N. appendiculata appendiculata,* 91, male tergite 10, dorsal view; 92, male tergite 10, lateral view; 93, 94, *N. minuscula,* 93, male tergite 10, dorsal view; 94, male tergite 10, lateral view; 95, 96, *N. schaeuffelei,* 95, cercus, lateral view; 96, hypogynial valve, medial view; 97, 98, *N. spatha,* 97, cercus, lateral view; 98, hypogynial valve, medial view; 99, 100, *N. nasuta,* 99, cercus, lateral view; 100, hypogynial valve, medial view.

dary development. (There is in my opinion no compelling reason to consider the dorsal ridge in *exastigma* and in the clade *astigma* to *submaculosa* a new structure, non-homologous with the major ridge of the other members of the *flavescens* group; cf. Oosterbroek 1980: 336, character 19A and B).

48. – Hypogynial valve: (0) minor ridge short (fig. 109); (1) posteriorly extended (fig. 110).

The minor ridge is elongate in the species *lempkei* and *submaculosa,* reaching towards the tip of the hypogynial valve.

49. – Sternite 9: (0) entire (fig. 112); (1) with break be-

tween its midposterior and anterolateral parts (fig. 111, arrowed).

The species *beckeri* and *cretensis* are the only representatives of the *flavescens* group that have a membranous interruption in between the broad anterolateral portion of sternite 9 and its slender posterior projection.

50. – Sternite 9: (0) yellowish coloured (fig. 111); (1) anteriorly blackish coloured, i.e. heavily sclerotized (fig. 112, arrowed).

Contrary to the other members of the group, the anterior margin of sternite 9 is blackish coloured in the species *minuscula* and *theowaldi*.

DISCUSSION OF ADOPTED PHYLOGENY

Phylogenetic analysis of the character state matrix given in table 2, with a zero-vector as outgroup, resulted in two most parsimonious trees with length 73, consistency index 68, and retention index 84. I used exact tree-calculating methods with both computer programs employed, viz. the 'ie' (implicit enumeration) command of HENNIG86 and the branch-and-bound algorithm of PAUP. The binary coded characters had the default weight 1. No a priori or a posteriori adaptations of the data were introduced to adjust the results of the analysis. Both programs produced the same pair of equally parsimonious trees.

The two trees obtained differ in the position of the species *flavescens*. It either is the sister species of a clade (*astigma* (*lempkei, submaculosa*)) or constitutes a trichotomy with *astigma* and the clade (*lempkei, submaculosa*). In the first tree character state 28(1) is considered an apomorphy for the clade (*astigma* (*lempkei, submaculosa*)), with subsequent reversal to the plesiomorphous state in *submaculosa*. The second tree depicts character state 28(1) as a homoplasy in the species *astigma* and *lempkei*. The second tree is topologically identical with the strict consensus tree which is shown in fig. 2.

The four most basal species in the cladogram split off consecutively. Next in the transition series follows the pair of sister species *beckeri* and *cretensis*.

The remainder of the cladogram contains several lineages of which the monophyly is only weakly corroborated.

The clade *exastigma* to *submaculosa* is substantiated by a single homoplasy, viz. the narrow anterior apodemes of the sperm pump, which are also found in the species *spatha* (character 30). The clade containing the species *exastigma* and the three subspecies of *guestfalica* is also relatively weakly supported by one homoplasy only (character 28). The character state involved, viz. the complete reduction of the sclerotized part of the ejaculatory duct, also occurs in the

two subspecies of *quadrifaria*, as well as in *astigma* and *lempkei*.

The clade *quadrifaria* to *theowaldi* is the third lineage within the cladogram of which the monophyly is demonstrated by a single homoplasy, in this case the bare sp2 (character 34). Within the *flavescens* group the same character state is known in the species *saccai* and *beckeri*.

In certain aspects the results of the phylogenetic analysis of the present paper differ considerably from those presented by Oosterbroek (1980: 333, cladogram 2B; see also Oosterbroek & Arntzen 1992). Fig. 113 shows the topology of Oosterbroek's cladogram of the *flavescens* group. For ease of comparison, the topology of the consensus tree of the present paper is given in fig. 114.

Oosterbroek (1980: 332) listed three synapomorphies in support of the monophyly of the *flavescens* group, two of which he considered weak and one strong. According to his views, the members of the *flavescens* group should be distinguished by a straightened dorsal margin of the gonocoxite ('dorsal margin of the male sternite nine is flattened'; Oosterbroek 1980: 332, character 10; considered weak). Oosterbroek noted that this character state is absent in the species *nasuta* and *spatha*. My observations demonstrate that the posterodorsal edge of the gonocoxite is curved also in *exastigma*, the three subspecies of *guestfalica* (cf. fig. 38) and in *schaeuffelei*. I therefore do not accept the straightened dorsal margin of the gonocoxite as a synapomorphy of the *flavescens* group.

The other two synapomorphies of the *flavescens* group distinguished by Oosterbroek are also used in the present paper. They are the presence of the membranous ridge underneath the free part of the crest (Oosterbroek 1980: 332, character 11; considered weak because of its presumed absence in *nasuta* and *guestfalica*, but see character 22 of the present paper) and the absence of the rods of the aedeagal guide (Oosterbroek 1980: 332, character 12; considered strong; cf. character 11 of the present paper).

Oosterbroek (1980: 332, characters 13 and 14; 346, character 2) distinguished *saccai* as the sister species of a clade containing the remainder of species and subspecies of the *flavescens* group. The monophyly of this latter clade was substantiated by the presence of a partly trifid aedeagus and the reduction of the sclerotized part of the ejaculatory duct.

However, contrary to Oosterbroek's (1980, 1985a) assertion, non-*flavescens* group species with a partly trifid aedeagus are known within *Nephrotoma*. East Palaearctic and Oriental *Nephrotoma* species showing this feature include *alticrista* Alexander, *dodabettae* Alexander, *inorata* Alexander, *integra* Alexander, *medioproducta* Alexander, *nigrohalterata* Edwards, *rajah* Alexander, and *subpallida* Alexander. These species
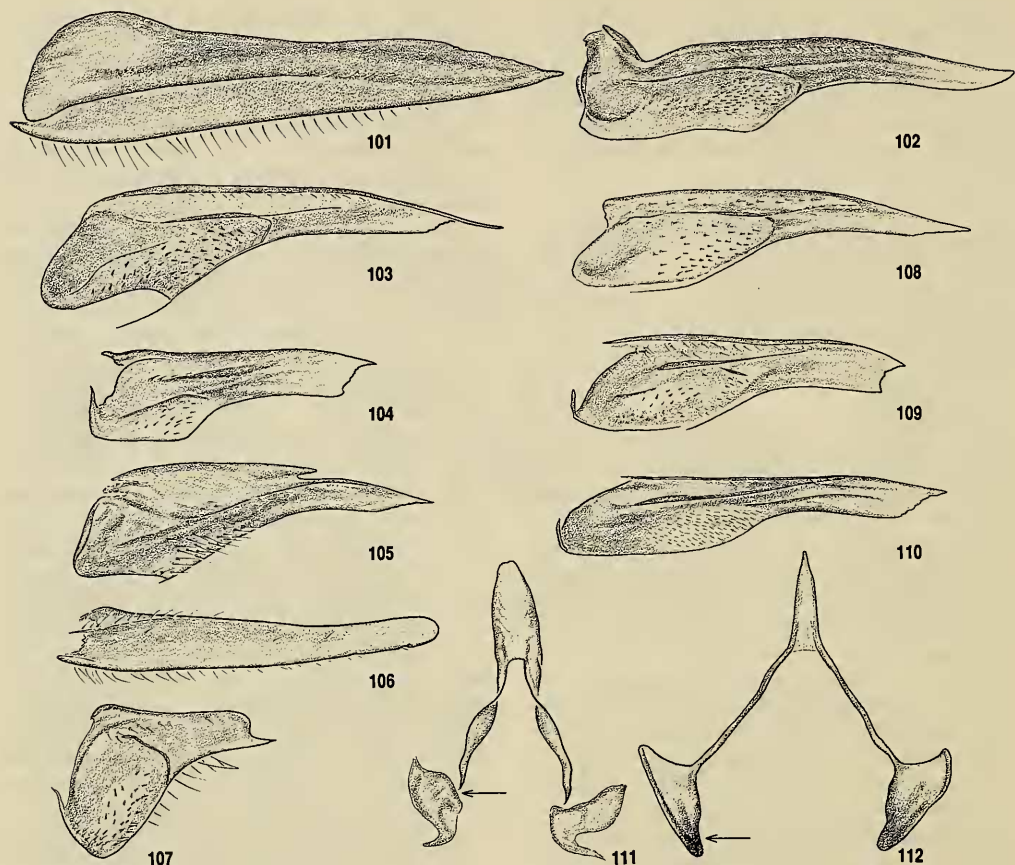
Figs. 101-112. – 101, 102, *N. saccai,* 101, cercus, lateral view; 102, hypogynial valve, medial view; 103, *N. beckeri,* hypogy-
nial valve, medial view; 104, *N. exastigma,* idem; 105, *N. guestfalica guestfalica,* idem; 106, 107, *N. quadrifaria quadrifaria,*
106, cercus, lateral view; 107, hypogynial valve, medial view; 108, *N. fontana,* idem; 109, *N. astigma,* idem; 110, *N. lempkei,*
idem; 111, *N. beckeri,* female sternite 9, dorsal view; 112, *N. minuscula,* idem.

do not belong to the *cornicina* group in its current
conception. It should be noted, moreover, that the
majority of the Afrotropical species of *Nephrotoma*
have the apical section of the aedeagus modified. The
apical portion in these species looks like a ribbon or a
flattened tube with sclerotized lateral margins, much
as in the east Palaearctic and Oriental species with a
trifid aedeagus, but then without the medial filament.
A partly trifid aedeagus, which is also known in spe-
cies of the tipulid subgenera *Tipula* (*Acutipula*
Alexander), *T.* (*Lunatipula* Edwards), *T.* (*Odonatisca*
Savchenko), *T.* (*Papuatipula* Alexander), and *T.*
(*Pterelachisus* Rondani) could well represent a plesio-
morphy in *Nephrotoma*. I therefore assume that the
structure of the aedeagus in *saccai*, which is tubular
throughout, represents an autapomorphy of the spe-
cies (cf. appendix). Likewise, the reduction of the
sclerotized part of the ejaculatory apodeme is evaluat-
ed differently in the present study (cf. characters 27
and 28).

In this context it should be noted that Oosterbroek
(1985a: 247) assigned the Japanese species *subpallida*
Alexander to the *flavescens* group on account of its
partly trifid aedeagus. When a trifid aedeagus is re-
garded a plesiomorphy on this level of analysis, the
feature - of course - advances no argument to incor-
porate any species in the *flavescens* group. Moreover,
the male of *subpallida* has well developed rods of the
aedeagal guide, a plesiomorphous character state not
found in the *flavescens* group (cf. character 11 of the
present paper). The ovipositor of *subpallida* has
blunt-tipped, well-developed cerci and large hypogy-
nial valves, both structures thus being of a different,
presumably plesiomorphous, type compared with the
cerci and hypogynial valves of the members of the *fla-
vescens* group (cf. characters 43 and 45 of the present

text). For these reasons I do not include *subpallida* in the *flavescens* group.

Next in Oosterbroek's transition series is the species *nasuta*, which was considered the sister species of the remainder of the *flavescens* group on account of the plesiomorphously large anterior apodemes of the sperm pump (cf. Oosterbroek 1980: 333, character 15). Reduction of the size of the anterior apodemes is employed in a slightly different manner and at another branching point in the present paper (cf. character 30).

The sister group of *schaeuffelei* in Oosterbroek's phylogeny is characterized by the serrate hypogynial valves (cf. Oosterbroek 1980: 333, character 16). However, incorporated in this clade is the species *spatha*, a species of which the female sex was unknown to Oosterbroek in 1980. The female of *spatha* was described by Eiroa & Novoa (1987) based on material collected in Galicia, Spain. It has the ventral margin of the tip of the hypogynial valve smoothly curved (fig. 98) and can therefore not be placed in the clade distinguished by the serrate hypogynial valve (cf. character 45 of the present paper). [Oosterbroek & Artzen (1992) excluded *spatha* from their cladogram of the *flavescens* group].

Figures 113 and 114 both depict the species pair *beckeri* and *cretensis* as the sister group of the remainder of species and subspecies of the *flavescens* group.

According to Oosterbroek's views, *guestfalica* and *quadrifaria* should be considered sister taxa. This relationship was postulated on account of the reduction of the hypogynial valves (Oosterbroek 1980: 334, character 16B), the shape of tergite 10 in the male (loc. cit.: 336, character 17P) and the presence of bristles on the alar squama (as 'neala'; loc. cit.: 336, character 18). The shape of the hypogynial valves of both species is very different (cf. figs. 105, 107). The same holds for the shape of male tergite 10 (cf. figs. 87-90, and characters 37 and 38 of the present paper). Although probably a plesiomorphy in the family Tipulidae, the presence of bristles on the squama is quite unique in the genus *Nephrotoma*. I have to assume that these bristles developed independently in both *guestfalica* and *quadrifaria*.

The position of the species *fontana* in the cladogram of Oosterbroek differs noticably from its allorted place in the consensus tree of the present text. The sister group of *fontana* is, according to Oosterbroek, characterized by the absence of the downcurved part of the minor ridge of the hypogynial valve (Oosterbroek 1980: 336, character 19). However, not all members of this 'sister group' lack the downcurved part of the minor ridge, viz. both subspecies of *appendiculata* and *flavescens* (fig. 10). My interpretation of the position and state of development of the ridges of the hypogynial valve, which deviates from

Oosterbroek's views, is explained under characters 47 and 48 of the present text.

The clade *appendiculata* to *theowaldi* of Oosterbroek fully concords with my ideas on the relationships of the species involved.

The exact phylogenetic relationship of the species *sullingtonensis* was left unresolved by Oosterbroek. On account of the shape of the gonapophysis of the aedeagal guide it can be considered to be more closely related with the species of the clade *astigma* to *submaculosa* (cf. character 9 of the present paper).

According to Oosterbroek, *exastigma* is closely related with the species of the clade *astigma* to *submaculosa*. He corroborated this postulate by the presence of both minor and major ridges of the hypogynial valves (Oosterbroek 1980: 336, character 19A, with the major ridge assumed to represent a newly developed structure), the short aedeagus (loc. cit.: 336, character 23), and the toothless claws in the male (loc. cit.: 337, character 24). The three characters are discussed under the respective characters 47, 13 and 1 of the present text. My argumentation results in a more basal position of *exastigma* in the *flavescens* group.

Oosterbroek's clade *astigma* to *submaculosa* is identical to the clade *astigma* to *submaculosa* presented here, inclusive of the trichotomy I was unable to resolve.

In summary, both our cladograms (figs. 113, 114) recognize the same basal species in the *flavescens* group, with the exception of the species *spatha*. In Oosterbroek's solution *spatha* occupies a more derived position. The same applies to *exastigma*, which is placed next to *spatha* in Oosterbroek's phylogeny. A sister group relationship of *guestfalica* and *quadrifaria*, as suggested by Oosterbroek, was not substantiated in the present study. The species *fontana* has a more derived position in my consensus tree. The trichotomy of which *sullingtonensis* forms part in fig. 113 is resolved in fig. 114. Here *sullingtonensis* is depicted as the sister species of the clade *fontana* to *submaculosa*. Both Oosterbroek's and my solutions agree on the composition of the clades *appendiculata* to *theowaldi* and *astigma* to *submaculosa*. Differences between figs. 113 and 114 are the result of selection and interpretation of characters. They do not represent artefacts of the analytical methods employed, viz. the 'manual' approach of Oosterbroek versus computational procedure of the present study.

DISTRIBUTION

In this section I will give a synopsis of the distribution of the species and subspecies of the *flavescens* group. For the time being, more detailed information can be found in Oosterbroek (1978, 1982, 1985b) and in Oosterbroek & Theowald (1992).
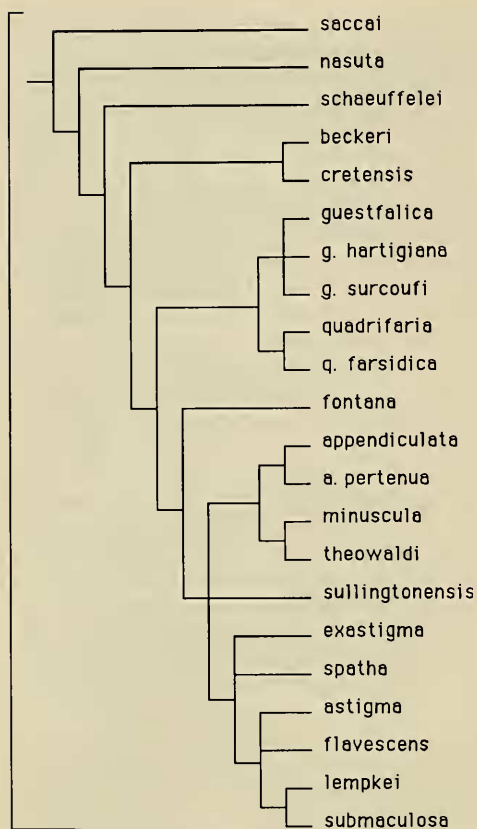
Left tree (Fig. 113):

- saccai
- nasuta
- schaeuffelei
- beckeri
- cretensis
- guestfalica
- g. hartigiana
- g. surcoufi
- quadrifaria
- q. farsidica
- fontana
- appendiculata
- a. pertenua
- minuscula
- theowaldi
- sullingtonensis
- exastigma
- spatha
- astigma
- flavescens
- lempkei
- submaculosa

Right tree (Fig. 114):

- schaeuffelei
- spatha
- nasuta
- saccai
- beckeri
- cretensis
- exastigma
- guestfalica
- g. hartigiana
- g. surcoufi
- quadrifaria
- q. farsidica
- appendiculata
- a. pertenua
- minuscula
- theowaldi
- sullingtonensis
- fontana
- astigma
- flavescens
- lempkei
- submaculosa

Fig. 113. (Left) Topology of the phylogeny of the *Nephrotoma flavescens* species group according to Oosterbroek (1980) and Oosterbroek & Arntzen (1992).

Fig. 114. (Right) Topology of the consensus tree of the *Nephrotoma flavescens* species group of the present paper.

The most basal species in the phylogeny of the *flavescens* group, *schaeuffelei*, is known from the Elburz mountains (Iran) and the Talysch mountains (Azerbaydzhan) to the south-west of the Caspian Sea.

The species *spatha* is endemic to north-west Spain. The species *nasuta* is known from a few localites in western, central and eastern Turkey, while *saccai* occurs in south-west Italy and northern Sicily.

The species pair *beckeri* and *cretensis* has an eastern Mediterranean distribution, with *beckeri* being distributed in Cyprus and the adjacent mainland of Turkey, as well as Lebanon and Israel. Its sister species is endemic to Crete.

The species *exastigma* is confined to northern Algeria and Tunisia.

The three subspecies of *guestfalica* are essentially west Mediterranean, with the nominate subspecies having the largest range of the three, extending from England and south Sweden in the northwest, Spain in the south-west to western Turkey in the east. The subspecies *guestfalica hartigiana* is endemic to
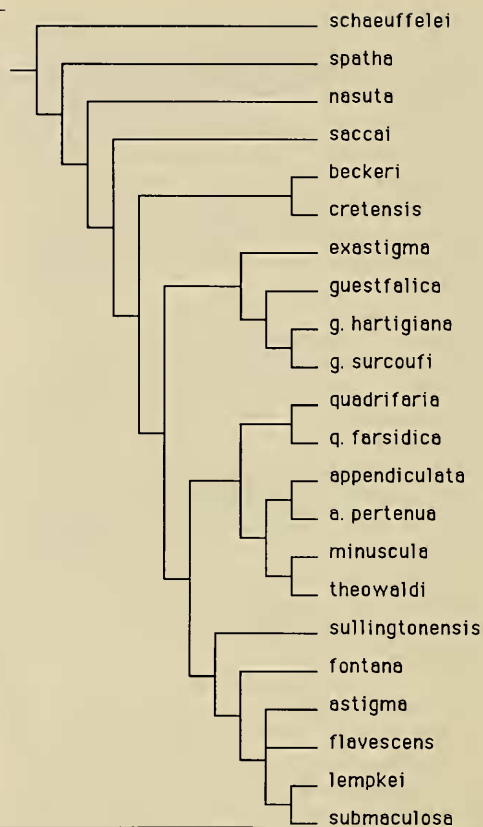
Sardinia, while the subspecies *guestfalica surcoufi* is distributed in Morocco, Algeria and Tunesia.

The nominate subspecies of *quadrifaria* is distributed over west and central Europe with its range extending towards the east over the Crimea peninsula and the Caucasus mountain range. The subspecies *quadrifaria farsidica* is known from north-west Iran in the area adjacent to the Caspian Sea.

The nominate subspecies of *appendiculata* is largely distributed over west and central Europe, eastwards reaching towards the westcoast of the Caspian Sea and southwards to Anatolia. It is absent from southwest Europe (Spain, Italy) where it is replaced by the subspecies *appendiculata pertenua*. In this context the occurrence of *appendiculata* sensu stricto on Sardinia is remarkable. The subspecies *appendiculata pertenua* is known from north-west Morocco and south-west Europe, including Corsica, Sicily and Malta. In its turn, this subspecies is absent from Sardinia. The species *minuscula* is known from Cyprus and the Levant, *theowaldi* occurs in south and south-west Turkey and

in the Greek island Rhodos.

The species *sullingtonensis* is distributed from northern Morocco through Spain and France to southernmost England. The species *fontana* is endemic to Algeria, while *astigma* is confined to the north of Algeria and Tunesia. Both *flavescens* and *submaculosa* are widespread throughout western and central Europe, with *submaculosa* occurring in Corsica, Sardinia, Sicily and the mainland of Italy. The species *flavescens* is absent in the four last mentioned areas. The species *lempkei* is at present known only from the islands Mallorca and Menorca.

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APPENDIX

In this section the recognized autapomorphies of the species and subspecies of the *Nephrotoma flavescens* group are listed.

appendiculata appendiculata: no autapomorphies recognized.

appendiculata pertenua: differing from nominal subspecies in details of male tergite 10 only.

astigma: shape of lateral shells of male tergite 10 in lateral view.

beckeri: shape of male tergite 10; shape of inner gonostylus.

cretensis: shape of compressor apodeme of sperm pump.

exastigma: lateral prescutal stripes straight; inner gonostylus with sclerotized ridge from anterior to lateral part.

flavescens: medial prescutal stripes with dull lateral margins, downcurved part of lateral prescutal stripes dull.

fontana: shape of extension of male sternite eight; shape of gonapophysis of aedeagal guide.

guestfalica guestfalica: position and shape of crest of inner gonostylus.

guestfalica hartigiana: crest of inner gonostylus partly reduced.

guestfalica surcoufi: crest of inner gonostylus entirely reduced.

lempkei: medial projection on male sternite eight slender, somewhat tapering towards tip.

minuscula: aedeagal guide with dorsolaterally extending ridges; form and length of central ridges of male tergite 10.

nasuta: nasus long; shape of male tergite 10; shape of aedeagus, particularly at branching point.

quadrifaria quadrifaria: shape of inner gonostylus; shape of male tergite 10.

quadrifaria farsidica: medial projection of male sternite eight directed dorsally.

saccai: shape of male tergite 10; shape of gonapophysis of aedeagal guide; sperm pump posteriorly with upcurved plate; aedeagus single throughout; genital fork reduced.

schaeuffelei: shape of inner gonostylus; outer gonostylus anteriorly with pubescent incurved swelling; shape of sp2.

spatha: hairs on vertex short; shape of male tergite 10.

submaculosa: no autapomorphies recognized.

sullingtonensis: prescutal stripes partly confluent.

theowaldi: aedeagus near branching point with pair of lateral extensions; crest of inner gonostylus twisted along its longitudinal axis.